The Ecological Role of Iron-Manganese Concretions in the Gulf of Finland

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Tiivistelmä – Referat – Abstract

Rautamangaanisaostumia muodostuu sekä syvänmeren että rannikkoalueiden pehmeille pohjille biogeokemiallisten ja mikrobisten reaktioiden seurauksena. On arvioitu, että saostumia esiintyisi jopa 11 %:lla Suomen merialueista. Saostumat muodostavat kovan alustan pääasiallisesti pehmeälle sedimenttipohjalle, lisäten merenpohjan geologista ja elinympäristön monimuotoisuutta. Näiden on havaittu korreloivan pohjaeliöstön monimuotoisuuden kanssa. Huolimatta saostumapohjien laajasta esiintymisestä, niiden merkitys meriekosysteemille on suurilta osin tuntematon. Viimeisimmässä Suomen luontotyyppien uhanalaisuusarvioinnissa rautamangaanisaostumapohjat määriteltiin puutteellisesti tunnetuksi luontotyypiksi.

Tutkimuksen tavoite oli tarkastella rautamangaanisaostumakenttiä Itämeren luontotyyppinä. Pohjan biodiversiteettiä tutkittiin kahdella lähestymistavalla: pohjan sessiiliä ja liikkuvaa eliöstöä tutkittiin pistesukelluksilla. Aineistoa vertailtiin Vedenalaisen meriluonnon monimuotoisuuden inventointiohjelmassa (VELMU) kerättyyn aineistoon. Sedimentistä otettiin näytteitä Van Veen -noutimella, ja aineistoa verrattiin ympäristötiedon hallintajärjestelmä Hertasta kerättyyn avoimeen tietoon

Saostumien määrä ja muoto vaikuttavat merenpohjan eliöstöön. Samankaltaisuudet pehmeiden sedimenttipohjien eliöyhteisöjen kanssa riippuvat pehmeän pohja-aineksen määrään elinympäristössä, mikä riippuu saostumien muodosta ja määrästä. Levymäiset saostumat vaikuttavat pohjan eliöstöön pyöreitä ja kiekkomaisia saostumia enemmän, sillä ne muodostavat saostumakentistä monipuolisimpia elinympäristöjä, jotka eroavat merkittävästi paljaasta merenpohjasta. Tutkimuksen perusteella saostumakenttiä ei välttämättä tulisi luokitella vain yhdeksi luontotyypiksi, sillä pohjan eliöstöyhteisöt ovat erilaisia eri saostumakentillä, riippuen saostumien muodosta.

Avainsanat – Nyckelord – Keywords
Rautamangaanisaostumat, Suomenlahti, elinympäristön monimuotoisuus, geodiversiteetti, biodiversiteetti, pohjaeläimet

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Tiivistelmä – Referat – Abstract

Iron-manganese (FeMn) concretions are found on soft sediment bottoms both in the deep sea and coastal sea areas, formed as a result of a combination of biogeochemical and microbial processes. It has been estimated that concretions occur at least in 11 % of the Finnish marine areas. Concretions form hard substrates on predominantly soft seafloors, and they are therefore suggested to increase geodiversity and habitat complexity of the seafloor. This has been found to correlate with biodiversity of the benthic fauna. Despite their widespread occurrence in the northern Baltic Sea, the ecological importance of FeMn concretions has been left unaddressed. In the recent assessment of threatened habitat types in Finland, concretion fields were classified as a data deficient habitat type.

The aim of this study is to examine the role of FeMn concretions as habitats in the Baltic Sea ecosystem. Benthic biodiversity was investigated utilizing two approaches; the abundance of mobile fauna and sessile macrofauna were studied with point-dives. The data was compared to pre-existing data from similar soft bottoms where there are no observations of concretions, collected in the Finnish Inventory Programme for the Underwater Marine Environment (VELMU). Samples for sediment in-fauna were taken with a Van Veen Grab Sampler, and additional data was gathered also from Environmental Information System HERTTA (administered by Environmental Administration).

The shape and quantity of concretions appear to affect the abundance of sediment in-fauna. Similarities to the invertebrate composition of soft sediment habitats depends of the soft sediment availability in the habitat, which is dependent on concretion shape and quantity. Crusts seem to affect the faunal composition more than spheroidal and discoidal concretions, as they offer the most complex habitats, significantly different from bare seafloors. Based on this study, the concretion fields should not necessarily be considered as just one habitat type, since the faunal composition appears to differ according to the shape of the concretions.

Avainsanat – Nyckelord – Keywords
Iron-manganese concretions, Gulf of Finland, habitat complexity, geodiversity, biodiversity, benthic macrofauna

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Introduction

Iron-Manganese Concretion Fields

Iron-manganese (FeMn) concretions are mineral precipitates common in the Baltic Sea. Globally, mineral precipitates can be found in both the deep-sea and shallow shelf areas. In the deep-sea, polymetallic nodules and crusts are the most common types of precipitates. In shallow shelf areas, such as the Baltic Sea, all mineral precipitates are typically referred to as concretions (Kaikkonen et al., 2019).

FeMn concretions are abundant in the Finnish waters; it has been estimated that concretions occur in at least 11 % of the Finnish marine areas (Kaikkonen et al., 2019). The term ‘concretion field’ refers to seafloor habitat with > 90 % coverage of concretions, irrespective of their shape (HELCOM, 2013). Concretion fields (Fig. 1) have been classified as a data deficient habitat type in Finland (Kotilainen et al., 2018); despite their widespread occurrence in the Northern Baltic Sea, their ecological importance has been left unaddressed (Kotilainen et al., 2017). Concretions form hard substrates on predominantly soft seafloors, and they are therefore suggested to increase habitat complexity and to provide shelter from seafloor erosion – thus affecting the composition of macrobenthic communities associated with FeMn concretion fields (Kaskela et al., 2017). This study aims to investigate the role of FeMn concretion fields as a component of benthic biodiversity in the Baltic Sea.

Figure 1. Concretion field containing discoidal and irregularly shaped FeMn concretions. Picture: Finnish Environmental Institute (SYKE).

Typically, concretions occur in elevated areas characterized by slow sedimentation rates (Varentsov and Pronina, 1973). Concretion formation is a combination of biogeochemical and microbial processes, which vary in different areas according to environmental conditions (Yli-Hemminki et al., 2014; Kuhn et al., 2017). Alternating oxidizing and reducing conditions in the sediment drive the chemical reactions resulting in concretion formation around solid nuclei, e.g. gravel (Gasparatos, 2012). This results in the formation of alternating layers of Fe and Mn- rich oxides (Winterhalter, 1980; Glasby et al., 1997). These reactions are supported by microbial reduction, especially in the case of Mn oxide formation (Yli-Hemminki et al., 2014). The shape of concretions (Fig. 2) is determined by various environmental factors, such as sedimentation, currents, and the slope of the seafloor (Table 1) (Zhamoida et al., 1996, 2004). Formation processes are slow; concretions grow approximately 0.003 – 0.3 mm a^{-1}. Spheroidal concretions can be 670–850 years of age, and larger, flat concretions may be up to 2500–3800 years old (Grigoriev et al., 2013).

Figure 2. FeMn concretions found in the Gulf of Finland vary in both size and shape. a) Concretion rings around small stones. b) Spheroidal/Buckshot shaped concretions. c) Partially dissolved concretions (discoidal/rings). d) Discoidal concretions. e) Pieces of FeMn crusts. Picture: Elli Leinikki.

Table 1. Characteristics of some differently shaped concretions (Ingri, 1985; Zhamoida et al., 1996; Glasby et al., 1997; Zhamoida et al., 2004, 2007)

Concretion shape	**Description**	**Size range (mm)**	**Depth range (m)**	**Environmental conditions**	**Average Mn:Fe ratio**
Spheroidal/ Buckshot	Irregular, spheroidal shaped formations	1 – 5	54 – 77	High currents	0.70
Discoidal	Horizontal layers around solid nuclei	10 x 7 x 0.5 – 50 x 35 x 3	31 – 52	Low sedimentation	0.55
Crusts	Cavernous surface texture, can pile up on each other and coalesce with other concretions	Up to 200 – 300	24 – 48	Low erosion	0.09

For the concretion forming processes to result in solid structures, oxygen needs to be present. The development of anoxic zones can result in the dissolution of concretions. The dissolution of concretions is dependent on both the ambient geochemical conditions as well as anaerobic microbial processes (Yli-Hemminki et al., 2016). Anoxia affects the microbial processes that affect the cycles of redox-sensitive metals of the seafloor, especially the microbial reactions which accelerate the release of Mn oxides. Although Mn oxides participate directly in the oxidation of Fe^{2+} and thus may inhibit the release of Fe during anoxia, stability of the concretions is compromised. In addition to iron (Fe) and manganese (Mn), concretions store large quantities of arsenic (As) and phosphorus (P). Bacterial communities associated with FeMn concretions also play a role in binding polycyclic aromatic hydrocarbons (PAHs) and crude oil (Yli-Hemminki et al., 2016; Reunamo et al., 2017). The dissolution of concretions results in the release of the elements stored in the concretions. The release of P also affects the N cycling in the bottom sediments (Yli-Hemminki et al., 2016).

Oxygen availability thus affects the depth range of concretion occurrence, which is around 10 – 70 m in the Gulf of Finland (Glasby et al., 1997). In the Gulf of Finland, hypoxic and anoxic zones frequently develop due to eutrophication and fluctuating halocline (Maximov, 2006). Eutrophication in the region is a vicious cycle, largely driven by increased nutrient input from rivers and atmosphere, which lead to an increase in sedimentation of organic matter, oxygen depletion in the bottom layer, and the internal loading of phosphorus (Stoicescu et al., 2019). For concretions, oxygen depletion can also be a result of sediment accumulations, and dissolving concretions can be found when they are buried under sediment layers greater than 50–100 mm.

In addition to oxygen depletion, FeMn concretion fields are threatened by anthropogenic activities, such as seabed mining (Kotilainen et al., 2018). As the demand for raw materials is increasing, the lack of knowledge about FeMn concretion fields can be problematic, since the economic potential of concretions may be significant. In the eastern Gulf of Finland in Russian marine areas, it has been estimated that concretion fields contain 175 000 tonnes of phosphorus, 11 million tonnes of iron, and 1 million tonnes of manganese (Zhamoida et al., 1996, 2007). Seabed mineral extraction is gaining attraction as terrestrial resources are becoming progressively scarce, and conservation efforts of the remaining mineral resources are increasing (Vidal et al., 2017; Kaikkonen et al., 2018). The ecological effects of seabed mining and ecosystem recovery after mining operations have been investigated more in deep-sea areas than shallow shelf sea areas (Bluhm, 1994; Vanreusel et al., 2016; Paul et al., 2018; Stratmann et al., 2018; Simon-Lledó et al., 2019). However, the full grasp of environmental effects remains uncertain. In the Eastern Gulf of Finland, some geological effects of industrial-scientific submarine mining operations have been studied (Zhamoida et al., 2017). Yet, the FeMn concretion fields of Gulf of Finland have not been properly characterized as a habitat type, and the possible ecological impacts are difficult to assess (Zhamoida et al., 2017; Kaikkonen et al., 2018).

Habitat Complexity

Habitat complexity usually refers to the existence of different elements that construct a habitat (Tokeshi and Arakaki, 2012). Terms 'substrate heterogeneity', 'topographical complexity', 'habitat architecture', 'habitat heterogeneity' and 'the diversity of structural elements' are also typically used to describe habitat complexity. It is one of the most important factors affecting biotic assemblages, yet an understanding of the underlying mechanisms that resulting in/shape habitat complexity is still lacking (Kovalenko et al., 2012). Assessment of habitat complexity usually includes spatial scale, as well as the diversity, size, density and arrangement of structural elements. It usually has positive effects on biodiversity or species richness, and the two main theories on the mechanisms of how habitat complexity influences ecosystems are:

a) a greater number of niches due to an increased amount of available microhabitats (MacArthur and MacArthur, 1961; Willis et al., 2005; Koivisto and Westerbom, 2010; Kovalenko et al., 2012), and

b) a greater surface area in the habitat (Heck and Wetstone, 1977; Willis et al., 2005).

Diversity of an ecosystem is usually considered a desired trait, as diversity typically enhances ecosystem stability and resilience (McCann, 2000). The factors that stabilize a community are typically related to either competition of shared resources (Lamy et al., 2020), or different responses to environmental conditions (McCann, 2000). Environmental stressors, such as climate change, affect ecosystems in various ways, but diverse ecosystems are usually more resistant to these changes, in the context of ecosystem productivity (Isbell et al., 2015). Habitat complexity has been observed to increase resources in an ecosystem; food, shelter, nesting sites and suitable environments of larval settlement (Holbrook et al., 1990; Angel and Ojeda, 2001). In this sense, habitat complexity supports ecological complexity – a greater number of niches is supported by a greater number of available microhabitats (B. Gratwicke and Speight, 2005; B. Gratwicke and Speight, 2005; Miller et al., 2012). Lack of shelter in plain, less complex habitats may lead to an increased predatory pressure (Gagnon et al., 2019). Shelter can be provided by crevices in coral reefs as well as dense vegetation coverage, but the functionality of a given structure? as a refuge depends on the size of prey. Crevices formed on coral reefs are most beneficial to relatively small-bodied fish (length < 10 cm), whereas dense vegetation coverage can provide shelter for smaller fauna, such as microcrustaceans (Diehl, 1992; Wilson et al., 2007).

Structural elements that construct a complex habitat consist of both abiotic and biotic components. Examples of biotic components are foundation species in ecosystems (e.g. kelp forests, seagrass meadows), which structure communities, promote biodiversity and stabilize ecosystem processes by creating locally stable environmental conditions (Lamy et al., 2020). Structural complexity varies between different types of components and is associated with increased species richness. This has been demonstrated in seagrass meadows, macroalgae, sponges, ascidians, mussels, and coral reefs (Nagelkerken et al., 2000; Sunday et al., 2017). Different macrophytes provide different levels of complexity to microhabitats, depending on their structure (Taniguchi et al., 2003; Warfe et al., 2008). On seagrass meadows, plant biomass has proven to have a more significant effect on biodiversity, as opposed to the number of seagrass species (Heck and Wetstone, 1977). This is likely due to the uniform structure of seagrass (regardless of the species), and thus the complexity of the habitat is a result of vegetation density. Constructing elements may also include sessile fauna; a common example would be encrusting animals (e.g. *Amphibalanus improvisus*, *Einhornia crustulenta*) or polyps on a shell of a blue mussel (*Mytilus trossulus x edulis*) (Bradshaw et al., 2003; Koivisto and Westerbom, 2010). The main mechanisms are always the same: the variety, abundance, and structure of habitat components increase habitat heterogeneity.

In assessment of habitat complexity, five key traits should be considered: scales of habitat complexity, the diversity of complexity-generating elements, the spatial arrangement, size and the abundance of elements (Tokeshi and Arakaki, 2012). Methods used in assessment are currently mostly photogrammetric, but visual methods have deemed appropriate in previous studies, especially with projects on coral reefs and the effects on reef fish (Polunin and Roberts, 1993; Gratwicke and Speight, 2005b; Wilson et al., 2007). Furthermore, complexity of a habitat should be determined comparing differences within similar habitat types. A tropical coral reef is not comparable with a FeMn concretion field based on structural complexity, including topographical heterogeneity and the diversity of complexity generating elements, as well as faunal diversity.

However, in the northern Baltic Sea, where the species diversity is generally low (Laine, 2003) concretions may offer an important structural component to the ecosystem, which may affect the faunal diversity significantly. In the deeper sites of the study the complexity generating elements consist mostly of concretions and soft sediment, and these sites may be comparable with deep-sea manganese nodule fields. In shallower areas investigated in sessile- and mobile fauna assessment, complexity of the habitat may additionally increase due to other types of hard substratum and (drift) macroalgae. Spatial arrangement on concretion fields may be quite homogenous, as the shapes of the concretions found on each site are usually very similar. Sizes of elements does vary, yet, this is depending on the shape of the concretions, as there is greater variability in concretion sizes in sites with crust shaped concretions (Zhamoida et al., 2017).

Possible effects of Iron-Manganese Concretions on Benthic Macrofauna

Geological diversity and habitat complexity of seafloor have been found to correlate with biodiversity in the northern Baltic Sea (A.M. Kaskela et al., 2017). FeMn concretions form hard substratum on predominantly soft seafloors, which makes concretion fields more complex habitats than bare seafloors in similar conditions. Thus, it can be hypothesised that especially sites with crusts or other larger concretions may significantly alter the bottom habitat and macrobenthic community composition. This would be the result of the fact that crust shaped concretions add to the habitat complexity by forming crevices and creating available microhabitats or additional surface area on the bottom for invertebrates and fish (Thiel et al., 1993).

On concretion fields, the soft sediment may be almost completely separated from the water column by a thick layer of crusts, possibly making the fauna associated with the habitat more typical to fauna occurring on hard substratum (Bonsdorff and Pearson, 1999). In addition, discoidal concretions may offer hard substratum in patches, and spheroidal and buckshot concretions can be seen to affect the mean grain size of the sediment. However, smaller spheroidal concretions are not likely to be suitable hard substratum for sessile fauna, as they are likely not stable enough for faunal settlement (Walters and Wethey, 1996; Shunatova et al., 2018). Therefore, it can be hypothesised that their role might be less significant. This study compares the faunal composition of concretion fields with the faunal composition of soft sediment seafloors in similar depths, considering some of the environmental factors that can also impact faunal composition.

Material and Methods

Study Sites

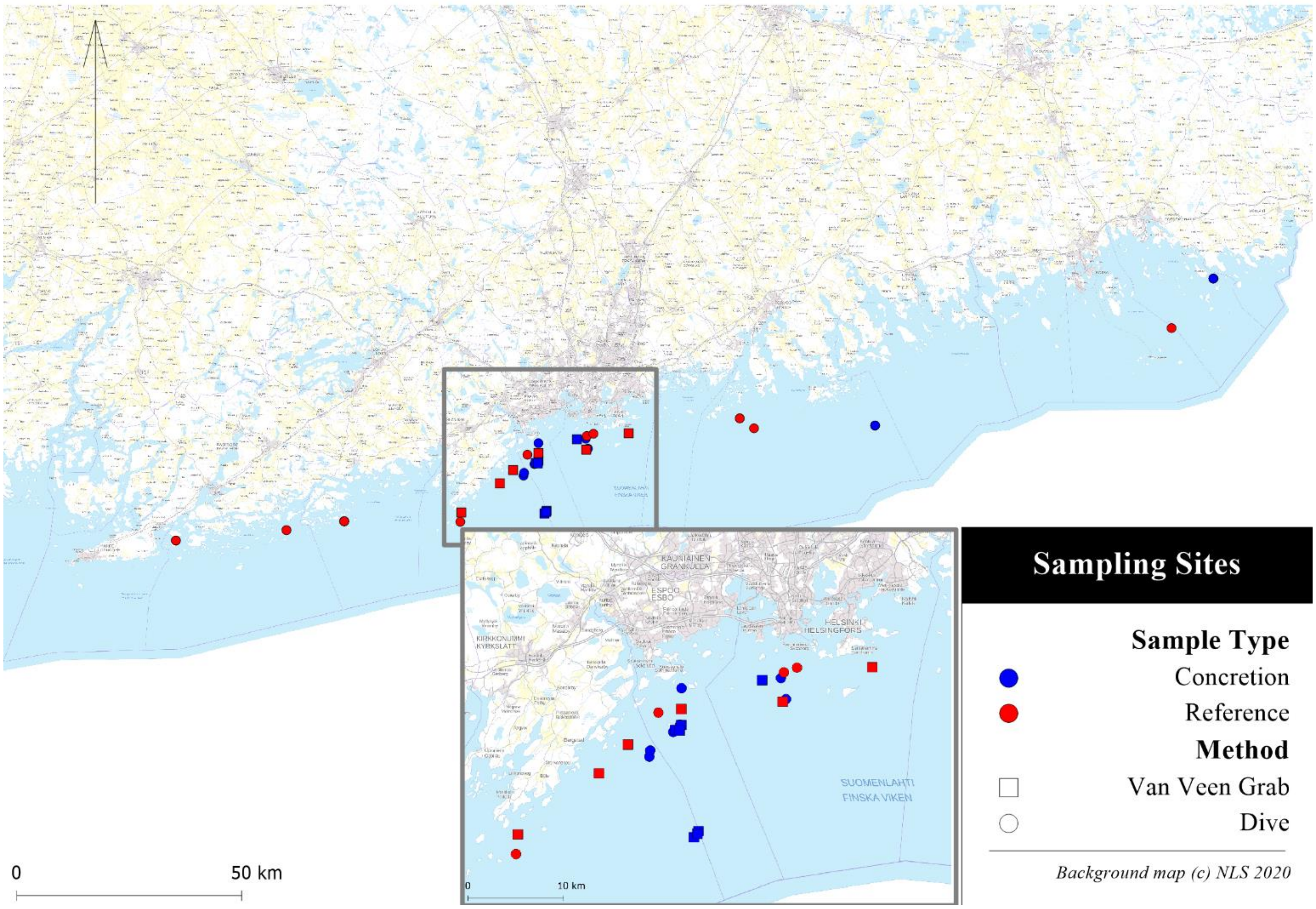

Figure 3. Study sites in the Gulf of Finland. Map created with Manifold 8.0.30.0. (Manifold Software Limited, 2017).

The study was conducted in the Gulf of Finland region, in Helsinki and Espoo archipelago in the June – August 2019 (Fig. 3). Sampling sites were selected based on pre-existing data from the Geological Survey of Finland. For sessile and mobile faunal sampling stations were selected based on concretion and bottom substratum observations and depth range – the sites should be accessible by SCUBA divers (10 – 30 m). For sediment infauna assessment, the stations were selected based on acoustic data and video observations made on R/V Geomari, from a depth range of 23 – 52 m.

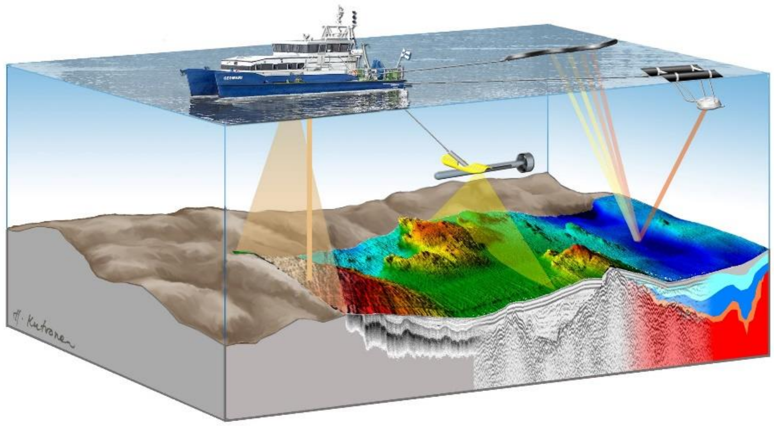

Figure 4. Acoustic methods used in geological seafloor mapping. Picture: Harri Kutvonen, Geological Survey of Finland.

In order to examine seafloor composition, seafloor was scanned utilising acoustic location methods: sediment echosouder, multibeam echosounder and a side-scan sonar (Fig. 4). Sediment echosounder (Pinger/MeriData with a 28 kHz sensor, Chirp/Meridata with a 4 kHz sensor) was used to assess depth, topography of the seafloor and the thicknesses of soft sediment layers, as well as the internal structures of different aged sediment layers (up to 10 cm accuracy). Multibeam echosounder was used to evaluate depth and topography from an area of at least the height of the water column from the both sides of the vessel (e.g. in a depth of 10 m, width of the scanned area is 60 m). In addition to depth and topography, multibeam echosounder provided information of the structure and coarseness (sediment grain size) of the seafloor (Simmons et al., 2017). A side-scan sonar (Klein 3000, 100 and 500 kHz, 75 m) was used to assess the topographical shapes of the seafloor, which included erosion and sedimentation structures, and anthropogenic traces, such as bottom trawling, dredging, anchoring, cables and shipwrecks (Kumudham and Rajendran, 2018).

Additional data from the Finnish Inventory Programme for the Underwater Marine Environment (VELMU) was used to complement sessile- and mobile fauna assessment. The data was gathered in the years 2014 and 2015 between June and August. Observations were selected from Gulf of Finland region (Helsinki, Espoo, Raasepori, Inkoo, Kirkkonummi, Porvoo, Kotka, and Hamina) based on similarities on bottom substratum and depth range (10 – 20 m). For sediment infauna assessment, additional data was gathered from the Environmental Information System HERTTA (administered by Environmental Administration), from Helsinki, Espoo, and Kirkkonummi, from a depth range of 23 – 30 m. The data was gathered in the years 2013 – 2015 between June and November.

Figure 5. Two divers ready for sessile and mobile fauna assessment. Picture: Mikko Kinnunen, Geological Survey of Finland.

Sessile and Mobile Fauna

Data on sessile and mobile fauna was collected with on point dives (Fig. 5): on each dive site three 4 m^2 transects were assessed, each transect placed ≥ 15 m apart from each other. On each transect depth (m), bottom substratum coverage (%), concretion coverage (%) and -shape (buckshot or spheroidal, discoidal, crust), and macrophytes coverage (%) were recorded. Sessile fauna was assessed as substratum specific coverage (%) on concretions, other hard substratum, soft substratum and macrophytes. Individuals of mobile fauna (e.g. *Saduria entomon*, fish) were counted during the observation period of 5 minutes. Data was collected using field data collection software Allure (Hautsalo, 2019) on an underwater tablet computer.

Figure 6. Benthic sampling on R/V Geomari with a Van Veen grab sampler. Picture: Satu Huurtomaa, Geological Survey of Finland.

Sediment Infauna

Sediment samples were taken with a Van Veen grab sampler (area 0.112 m^2, Fig. 6) on R/V Geomari (GTK). Van Veen grab sampler has a rectangular bite profile and is well suited for sediment infauna sampling in the Baltic Sea region, as over 90 % of benthic fauna is typically within the top 40 – 50 mm of the sediment (Riddle, 1989) . Large concretions were removed from the rest of the samples, rinsed thoroughly and stored separately to avoid crushing the fauna. Samples were homogenized and sieved through 1 mm (macrofauna) and 0.5 mm (meiofauna) sieves. Fractions were preserved in > 70 % EtOH (Wetzel et al., 2005). Macro- and meiofauna were identified and weighed in a laboratory.

Methods for Assessing Habitat Complexity

Complexity of a habitat is usually determined based on a few key factors: topography, height, rugosity and the number of refuge holes. As previously mentioned, when measuring habitat complexity, Tokeshi and Arakaki (2012) stressed that at least five traits that need to be considered in the assessment:

1. Scales of habitat complexity
2. Diversity of complexity-generating elements
3. Spatial arrangement of elements
4. Size of elements
5. Abundance or density of elements

In sessile and mobile fauna assessment, habitat complexity was measured as the coverage of habitat constructing elements on each transect. This included the coverage of concretions and other hard substratum types, soft substratum and possible presence of (drift) macrophytes and macroalgae. Substratum was later divided into two categories based on grain size: hard (> 2.0 – 60 mm, "Gravel") and soft substratum (Table 2). Concretions were included in the hard substratum in statistical analysis.

Table 2. Sediment grain size and category division (ISO 14688-1:2002).

Size class	**Large boulder**	**Medium boulder**	**Small boulder**	**Large stone**	**Small stone**	**Gravel**	**Sand**	**Silt**	**Clay**	**Mud**
Scale (mm)	> 3000	1200-3000	600-1200	100-600	60 - 100	2.0 - 60	0.06-2.0	0.002-0.06	< 0.002	< 0.002
Category	Hard substratum						Soft substratum			

In sediment infauna assessment, concretions were dried and weighed, but ultimately concretion quantity was measured on a scale of 0 – 3, (0 = no concretions present, 1 = some concretions present; 2 = a large quantity of concretions present, soft substratum (Table 2) visible; 3 = a great abundance of concretions, no soft substratum visible), matching to the pre-existing data gathered from HERTTA. The shape of the concretions was divided into four categories: buckshot shaped concretions, which included all spheroidal shaped concretions, crusts, discoidal and dissolving discoidal concretions.

Statistical Analysis

Welch's *t* test was used to compare differences in faunal coverage, density and number of species between concretion fields and bare seafloor. Nested ANOVA (analysis of variance) was used to determine the variances in faunal density and number of species, and the effect of concretion shape and quantity, and depth. Nested model was used to assess the variation between duplicates within each site. For the data from sessile and mobile fauna assessment, one-way ANOVA was used to determine the variances in the coverage of sessile fauna and number of species, and the effect of concretion and hard substratum coverage (%), as well as depth. Linear correlation between depth and faunal abundance was also tested. In sediment infauna assessment the factors determining habitat complexity are concretion quantity (0 – 3) and concretion shape (buckshot, crust, discoidal or dissolving discoidal), as no other hard substratum was present on these sites. Statistical analysis was conducted using RStudio 1.2.1335 (RStudio Team, 2018), with ggplot2 (Wickham, 2016), magrittr (Bache and Wickham, 2014) and ggpubr (Kassambara, 2020) packages.

Results

Sessile and Mobile Fauna

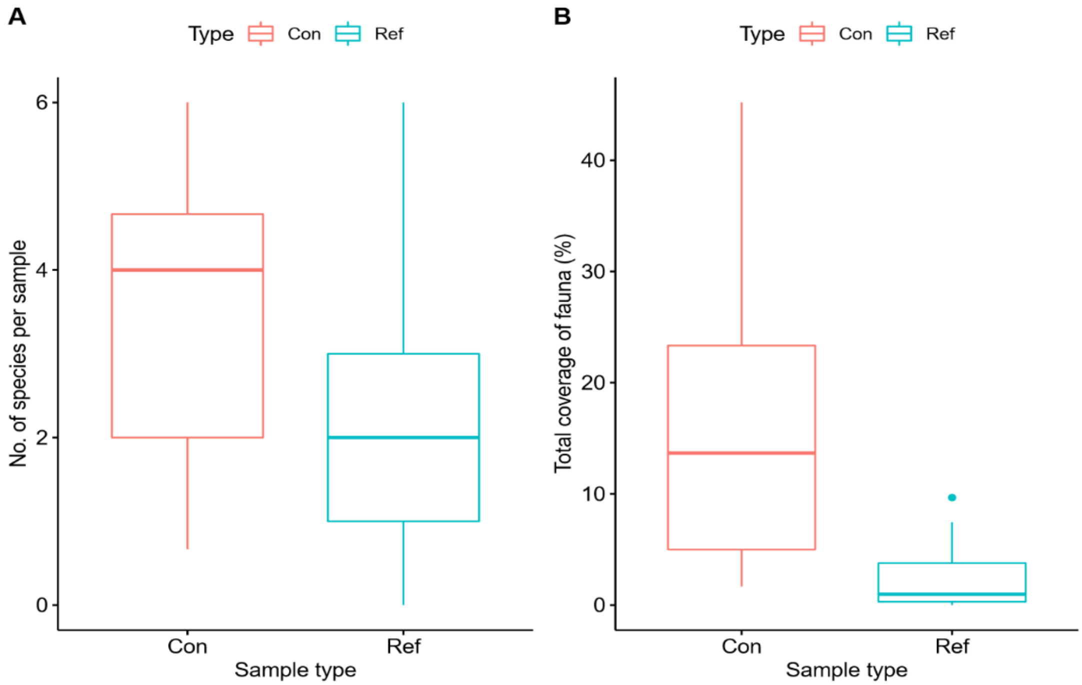

Figure 7. A) Sample type vs. number of species ($t(24.385) = 2.004$, $p = 0.056$, 95% CI, -0.036 to 2.572). **B)** Sample type vs. total coverage of fauna ($t(12.732) = 3.9054$, $p = 0.002$, 95% CI, -1.864 to 0.964). Sample type: Con = Concretions present, Ref = Concretions absent.

In sessile and mobile fauna, the mean number of species was higher on concretion fields (3.561) than reference sites (2.296), but the difference is not statistically significant ($p = 0.056$). Observations from the reference sites were also more scattered. Significant differences between the sample type and the mean coverage of fauna were found, mean coverage of fauna on concretion fields being 17.600 % and 2.238 % on reference sites (Fig. 7).

Table 3. Species found in the sessile and mobile fauna assessment, and the average coverage of said species on reference and concretion sites.

	Reference	**Concretion**
Annelida		
Worm pipes	12.5	8.333
Arthropoda		
Amphibalanus improvisus	0.514	7
Saduria entomon	1	2.083
Bryozoa		
Einhornia crustulenta	0.28	1.215
Chordata		
Pisces sp.	2	
Pomatochistus sp.	2	2
Zoarces viviparus	1.333	
Cnidaria		
Cordylophora caspia	2.025	7.333
Polyps	0.117	5.833
Mollusca		
Cerastoderma glaucum	0.051	1.867
Dreissena polymorpha	0.1	
Embletonia pallida	2.25	
Limecola balthica	0.300	3.014
Mya arenaria	0.501	1
Mytilus trossulus x edulis	1.104	7.405

Species were found in six phyla: Annelida, Arthropoda, Bryozoa, Chordata, Cnidaria and Mollusca (Table 3). Identifications were made on species level in two species of arthropods, one species of bryozoans, one species of chordates (fish), one species of cnidarians and six species of molluscs. Organisms that were not identified to species level were annelids, some polyps, fish larvae and the fish in the genus *Pomatochistus.* The average densities of hard-substratum species (bivalve *M. trossulus x edulis*, *Cordylophora caspia* and other polyps) were higher on concretion sites.

Table 4. Results of ANOVA testing the effect of concretion and hard substratum coverage (%) on the number of species and the total coverage of fauna (%). Concretion coverage (%) = CC, Hard substratum coverage (%) = HC.

	Number of species			**Total coverage of fauna (%)**		
	df	***F***	***P***	**df**	***F***	***P***
Effect of substratum coverage						
CC	1	0.027	0.8723	1	0.8826	0.3677
HC	1	5.8511	0.02207	1	23.108	$4.335e^{-05}$
Effect of substratum coverage + depth						
CC	1	0.0285	0.8693	1	0.8265	0.3847
+ *Depth (m)*	1	1.5886	0.2361	1	0.3006	0.5955
HC	1	6.1228	0.01967	1	22.3188	$5.893e^{-05}$
+ *Depth (m)*	1	2.3467	0.13677	1	0.0091	0.9245

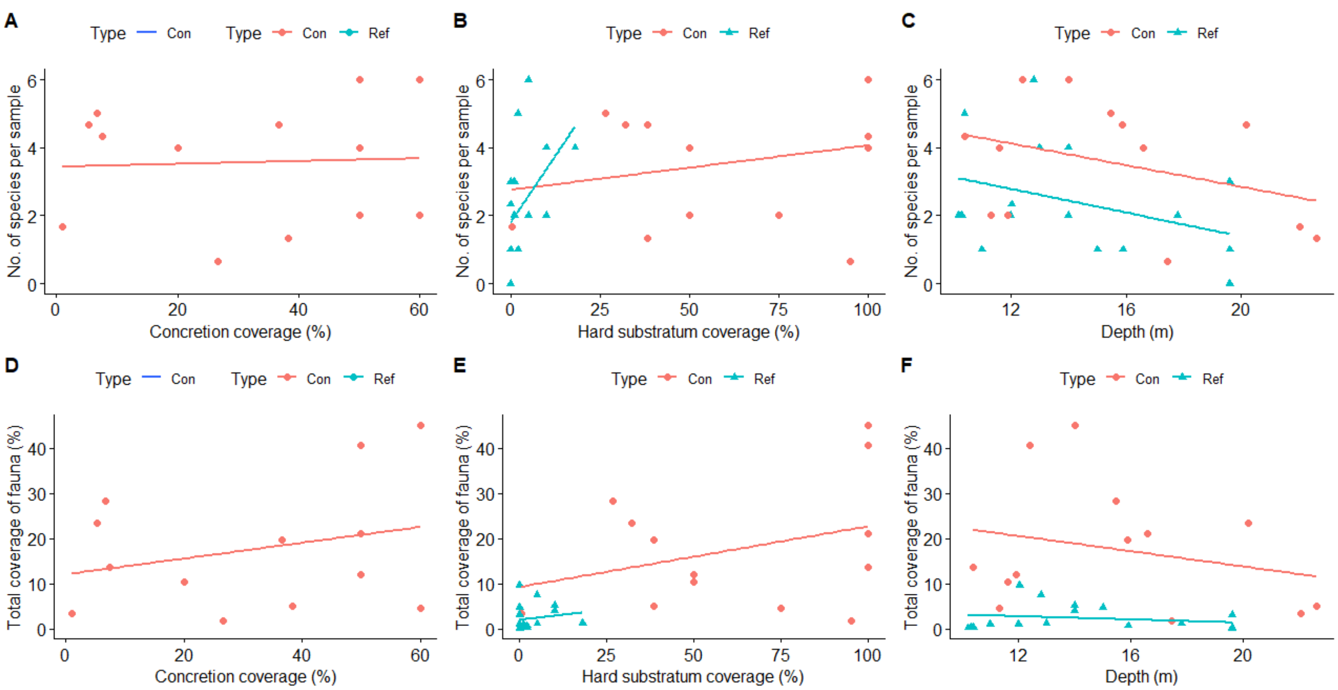

Figure 8. A) Number of species per sample vs. concretion coverage (%). **B)** Number of species per sample vs. hard substratum coverage (%). **C)** Number of species per sample vs. depth (m) (linear correlation: $F(1,29) = 3.237$, $p = 0.082$, $R^2 = 0.100$). **D)** Total coverage of fauna (%) vs. concretion coverage (%). **E)** Total coverage of fauna (%) vs. hard substratum coverage (%). **F)** Total coverage of fauna vs. depth (m) (linear correlation: $F(1,46) = 0.264$, $p = 0.611$, $R^2 = 0.009$). Sample type: Con = Concretions present, Ref = Concretions absent.

Concretion coverage itself did not affect the number of species or the total coverage of sessile fauna (Fig. 8 A, D). However, hard substratum coverage (%), including concretions, significantly affected both the number of species and the total sessile faunal coverage (Table 4, Fig. 8 B, E). Depth also had a negative linear correlation with the number of observed species (Fig. 8), and it strengthened the effect of hard substratum coverage on faunal abundance (Table 4).

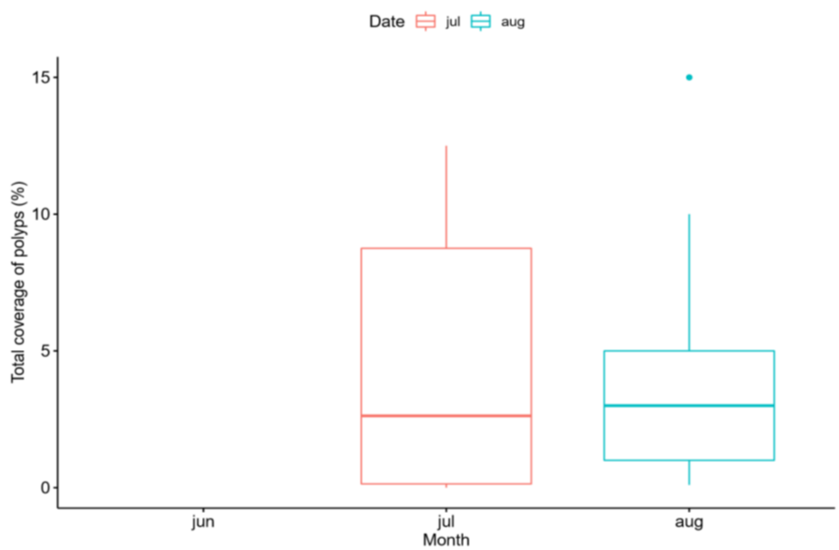

Figure 9. Observed succession of polyps in the Gulf of Finland ($t(8.265) = 0.052$, $p = 0.960$, 95% CI, -5.778 to 6.046).

Annual succession of polyps was observed; no polyps were present in the assessments made in June, and the mean coverage increased in July (4.642 coverage (%)) and August (4.508 coverage (%)) (Fig. 9). The polyp coverage mean was a little higher in August, and the observations were more scattered in July. However, the result from the *t* test was not significant ($p = 0.960$).

Sediment Infauna

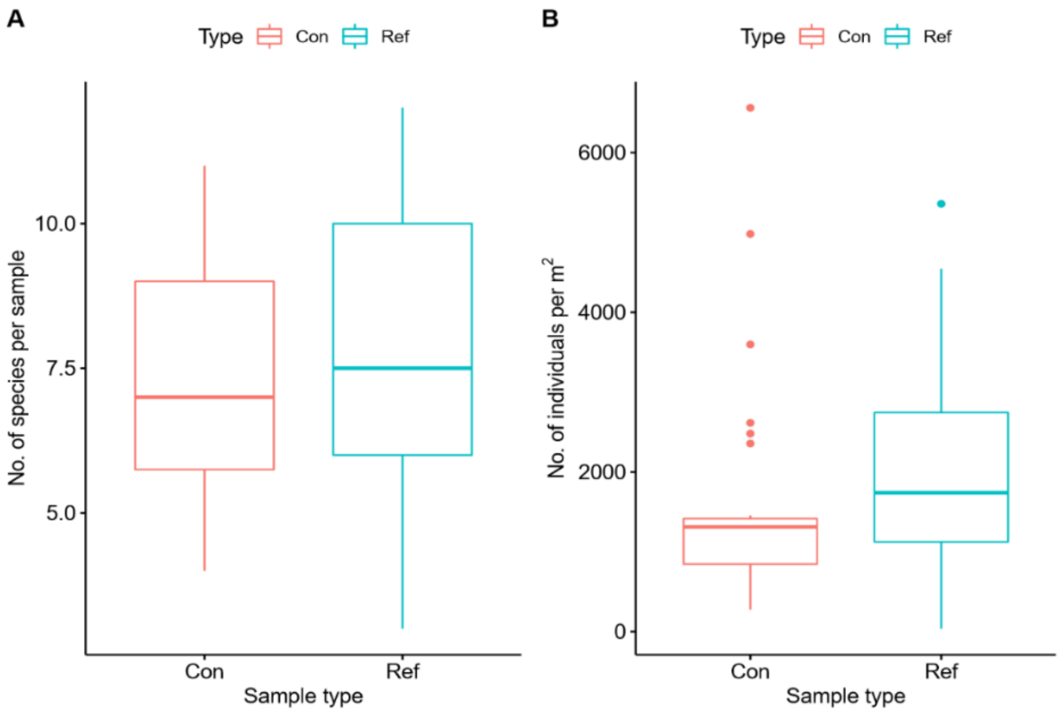

Figure 10. A) Sample type vs. number of species ($t(34.563) = -0.646$, $p = 0.522$, 95% CI, -1.864 to 0.964). **B)** Sample type vs. number of individuals m^{-2} ($t(40.542) = -1.141$, $p = 0.261$, 95% CI, -1329.493 to 369.967). Sample type: Con = Concretions present, Ref = Concretions absent.

Compared to results on sessile- and mobile faunal assessment, sample type did not affect the abundance of sediment infauna significantly (Fig. 10). The mean number of species was higher on reference (7.70) than concretion sites (7.25), and the mean number of individuals per m^2 (ind. m^{-2}) was higher on reference sites (2062.360 ind. m^{-2}) than concretion sites (1582.597 ind. m^{-2}). However, the observations on faunal densities were more scattered on concretion sites.

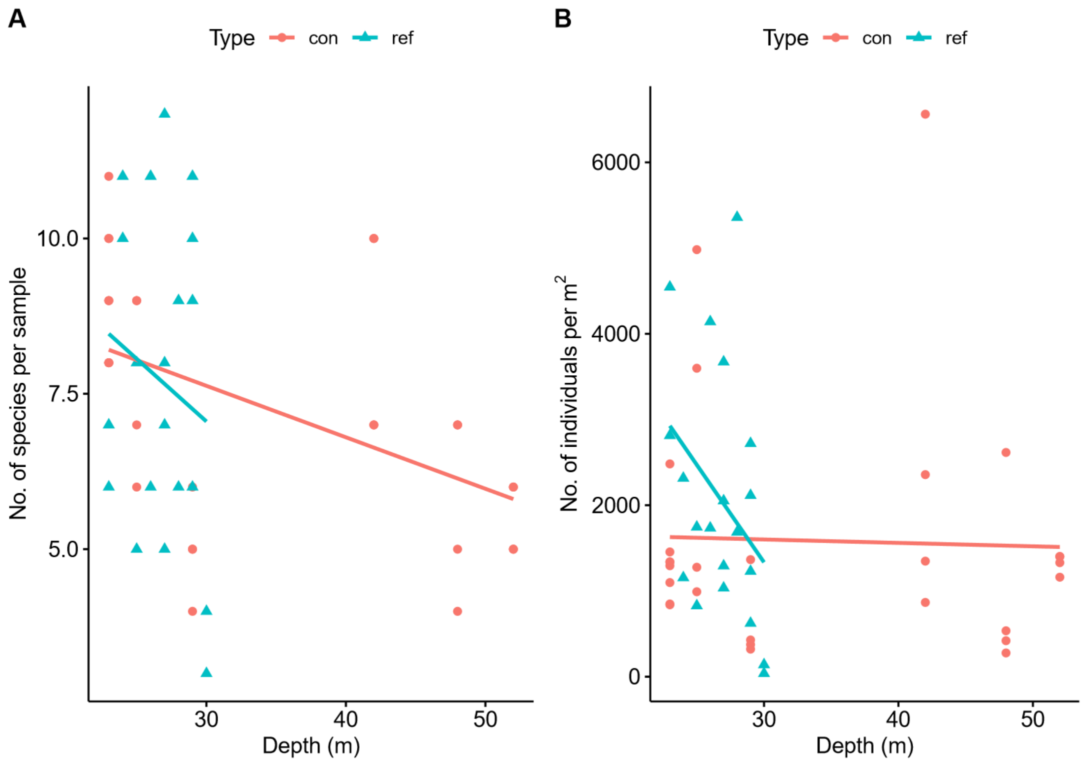

Figure 11. The effect of depth on **A)** Number of species per sample ($F(1,46) = 6.508$, $p = 0.0141$, $R^2 = 0.124$). **B)** Number of individuals per m^2 ($F(1,46) = 0.682$, $p = 0.413$, $R^2 = 0.0146$). Sample type: Con = Concretions present, Ref = Concretions absent.

In parallel to the observations in sessile- and mobile fauna assessment, increase in depth had a linear correlation with the decrease in both the number of species per sample ($p = 0.0141$) as well as the number of individuals per m^2 ($p = 0.413$) (Fig. 11). Reference sites were generally shallower than concretion sites (Concretion sites: 23 – 52 m; Reference sites: 23 – 30 m).

Table 5. Results of Nested ANOVA testing the significance of concretion shape and quantity on the number of species and number of individuals per m^2 in different phyla.

	Number of species			Number of individuals per m^{-2}		
	df	***F***	***P***	**df**	***F***	***P***
Effect of concretion shape						
Shape	3	13.1869	0.000230	3	0.2412	0.86612
Site	3	8.5909	0.001749	3	2.5629	0.09649
Site:Sample	7	2.1515	0.105374	7	0.5902	0.75377
Effect of concretion quantity						
Quantity	1	0.6488	0.427857	1	0.6982	0.4110
Site	14	3.3307	0.003887	14	1.5863	0.1498
Site:Sample	6	0.9675	0.466312	6	0.7790	0.5938
Effect of concretion shape + depth (m)						
Shape	3	13.1869	0.0002300	3	0.2412	0.86612
Depth	1	24.6795	0.0002065	1	6.9878	0.01927
Site	2	0.5466	0.5907706	2	0.3505	0.71033
Site:Sample	2	2.1515	0.1053744	7	0.5902	0.75377
Effect of concretion quantity + depth (m)						
Quantity	1	0.7810	0.3852544	1	0.6742	0.4194
Depth	1	15.5011	0.0005821	1	0.1709	0.6828
Site	14	3.3522	0.0040922	16	1.5273	0.1724
Site:Sample	6	1.1647	0.3561287	6	0.7523	0.6135

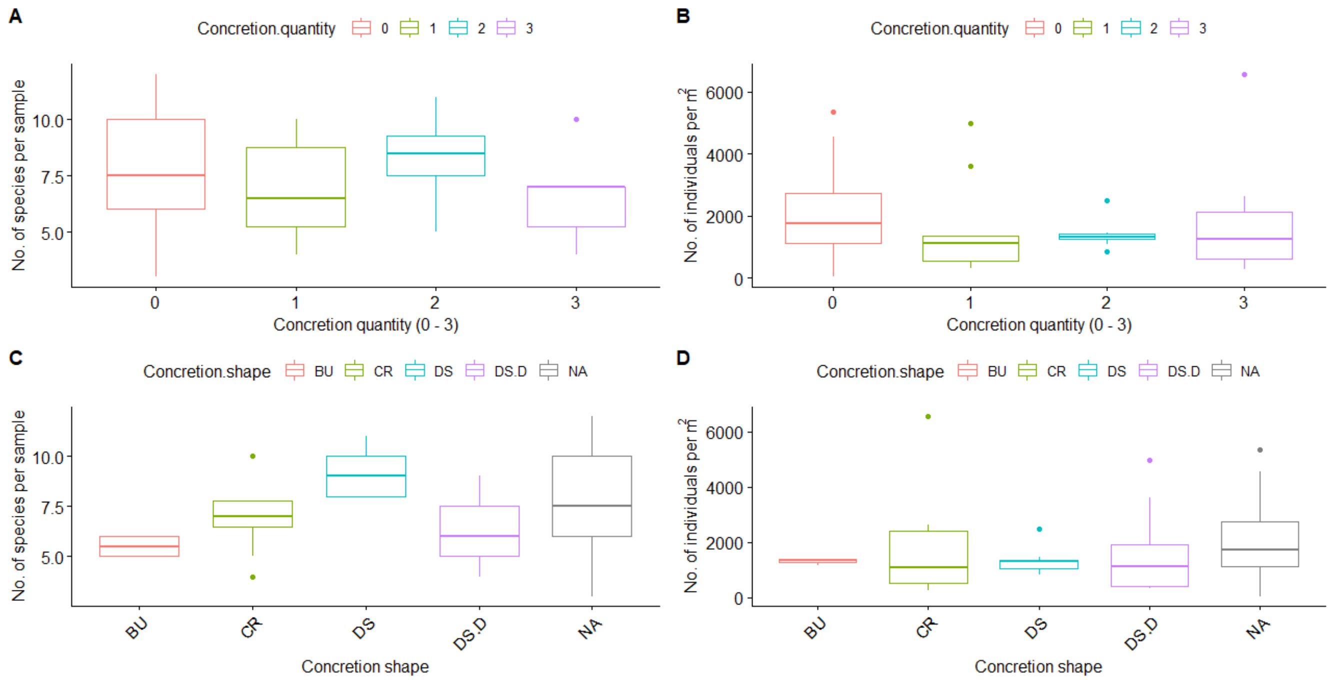

Figure 12. A) Number of species vs. concretion quantity (0 – 3). **B)** Number individuals per m^2 vs. concretion quantity (0 – 3). **C)** Number of species vs. concretion shape. **D)** Number of individuals per m^2 vs. concretion shape. Concretion shape: BU = Buckshot/Spheroidal, CR = Crust, DS = Discoidal, DS.D = Dissolving discoidal.

Both the concretion shape and quantity affected the mean number of species observed on the samples. The sites with the highest mean number of species were sites with crusts (7.125) or discoidal shaped concretions (9.125) (Fig. 12). However, since depth affected the faunal abundance (Fig. 11), it should be noted that the sites with crust shaped concretions were deeper (42 – 48 m) than sites with discoidal concretions (23 m). Depth also enhanced the effect of concretion shape on faunal abundance (Table 5). Neither the concretion shape nor quantity affected the mean number of individuals per m^2 significantly. Dissolving concretions were found 6 – 8 cm deep in the sediment, and the sediment was possibly hypoxic or even anoxic.

Table 6. Species found in the infauna assessment, and the average number of species and density of fauna. Concretion shape; Ref. = Reference, no concretions, BU = Buckshot, CR = Crust, DS = Discoidal, D.DS = Dissolving discoidal.

Species presence / average number of species						**Average density of macrofauna individuals m^{-2}**					
Sample type	**Reference**			**Concretion**		**Sample type**	**Reference**			**Concretion**	
Average no. of species	**7.7**			**7.25**		**Average density**	**112.617**			**155.992**	
Concretion shape	**Ref.**	**BU**	**CR**	**DS**	**D.DS**	**Concretion shape**	**Ref.**	**BU**	**CR**	**DS**	**D.DS**
Average no. of species	7.7	5.5	7.125	9.125	6.375	**Average density**	112.617	138.617	227.636	98.197	159.519
Annelida average	1.9	2.5	2.375	2.875	1.75	**Annelida average**	257.113	495.540	79.616	106.667	367.934
Hediste diversicolor	x					*Hediste diversicolor*	3.000				
Marenzelleria spp.	x	x	x	x	x	*Marenzelleria spp.*	827.742	991.071	225.446	242.188	960.938
Nematoda	x					*Nematoda*	9.328				
Oligochaeta	x		x	x	x	*Oligochaeta*	188.381		13.393	75.255	142.857
Polychaeta		x	x	x	x	*Polychaeta*		0.009	0.009	2.559	0.009
Arthropoda average	3.25	2.00	3.13	2.88	2.38	**Arthropoda average**	31.964	66.592	345.010	73.242	132.812
Bylgides sarsi		x	x	x		*Bylgides sarsi*		8.929	14.881	8.929	
Calliopius laeviusculus		x	x	x		*Calliopius laeviusculus*		17.857	85.714	62.5	
Chironomidae	x				x	*Chironomidae*	9.165				8.929
Copepoda	x	x				*Copepoda*	35.714	8.929			
Corophium volutator	x			x		*Corophium volutator*	13.261			8.929	
Gammarus spp.	x					*Gammarus sp.*	4.500				
Jaera spp.	x			x	x	*Jaera spp.*	3.000			15.625	8.929
Monoporeia affinis	x	x	x	x	x	*Monoporeia affinis*	82.165	292.411	755.580	143.973	93.75
Mysis mixta	x					*Mysis mixta*	3.000				
Mysis relicta	x					*Mysis relicta*	6.164				
Neomysis integer	x					*Neomysis integer*	4.500				
Ostracoda	x	x	x	x	x	*Ostracoda*	180.553	26.786	1475.446	279.018	629.464
Pontoporeia femorata			x	x	x	*Pontoporeia femorata*			23.809	26.786	35.714
Saduria entomon	x	x	x	x	x	*Saduria entomon*	13.334	17.857	51.339	40.179	20.089
Bryozoa average	0.00	0.00	0.00	0.50	0.00	**Bryozoa average**				0.009	
Einhornia crustulenta				x		*Einhornia crustulenta*				0.009	
Mollusca average	1.70	0.50	1.00	1.88	1.25	**Mollusca average**	172.665	13.393	34.970	179.129	73.661
Cerastoderma glaucum	x					*Cerastoderma glaucum*	43.290				
Hydrobia	x					*Hydrobia*	3.000				
Limapontia capitata	x					*Limapontia capitata*	24.002				
Limecola balthica	x	x	x	x	x	*Limecola balthica*	935.164	13.393	56.548	618.304	241.071
Mytilus trossulus x edulis	x		x	x	x	*Mytilus trossulus x edulis*	3.600		13.393	62.5	8.929
Potamopyrgus antipodarum	x			x	x	*Potamopyrgus antipodarum*	26.931			8.929	17.857
Theodoxus fluviatilis				x	x	*Theodoxus fluviatilis*				26.786	26.786
Priapulida average	0.85	0.50	0.63	1.00	1.00	**Priapulida average**	57.777	8.929	16.071	46.875	37.946
Halicryptus spinulosus	x	x	x	x	x	*Halicryptus spinulosus*	57.777	8.929	16.071	46.875	37.946

In the sediment infauna assessment, species were found in five phyla: Annelida, Arthropoda, Bryozoa, Mollusca and Priapulida (Table 6). Identifications were made on species level in one annelid species, ten species of arthropods, one species of bryozoans, six species of molluscs and one species of priapulids. Organisms that could not be identified to species level were annelids in the genus *Marenzelleria*, nematodes, oligochaetes and some polychaetes, arthropods in the genus *Gammarus* and *Jaera*, chironomid larvae, copepods and ostracods, as well as *Hydrobia* spp. molluscs.

The densities of *M. trossulus x edulis* were highest on sites with crusts (13.393 ind. m^{-2}) and discoidal shaped concretions (62.5 ind. m^{-2}). *Limecola balthica* densities were highest on reference sites (935.164 ind. m^{-2}), and of concretion sites, the average densities were higher on sites with discoidal (618.304 ind. m^{-2}) and dissolving concretions (241.071 ind. m^{-2}). *Monoporeia affinis* and Ostracoda densities were highest on sites with crusts (*M. affinis* 755.580 ind. m^{-2}, Ostracoda 1475.446 ind. m^{-2}). The average density of *Marenzelleria* spp. polychaete worms was high on these sites with buckshot shaped (991.071 ind. m^{-2}) and dissolving discoidal concretions (960.938 ind. m^{-2}). Oligochaete worms' densities were highest on reference sites (188.381 ind. m^{-2}) and sites with dissolving concretions (142.857 ind. m^{-2}) (Table 6).

Table 7. Results of ANOVA testing the significance of concretion shape and quantity on the number of species and number of individuals per m^2 in different phyla.

	Concretion shape			**Concretion quantity**		
	df	***F***	***P***	**df**	***F***	***P***
Number of species						
Annelida	3	2.4017	0.0926	1	4.3153	0.04338
Arthropoda	3	3.0845	0.04638	1	0.7415	0.3937
Bryozoa	3	5.7143	0.004246	1	1.0479	0.3113
Mollusca	3	2.4258	0.09032	1	2.755	0.1038
Priapulida	3	3.4286	0.0331	1	2.3701	0.1305
Number of individuals per m^{-2}						
Annelida	3	2.8015	0.06155	1	5.4909	0.02349
Arthropoda	3	2.6584	0.07116	1	10.174	0.002565
Bryozoa	3	5.7143	0.004246	1	1.0479	0.3113
Mollusca	3	4.7525	0.009699	1	12.547	0.0009226
Priapulida	3	5.4652	0.005232	1	12.774	0.0008387

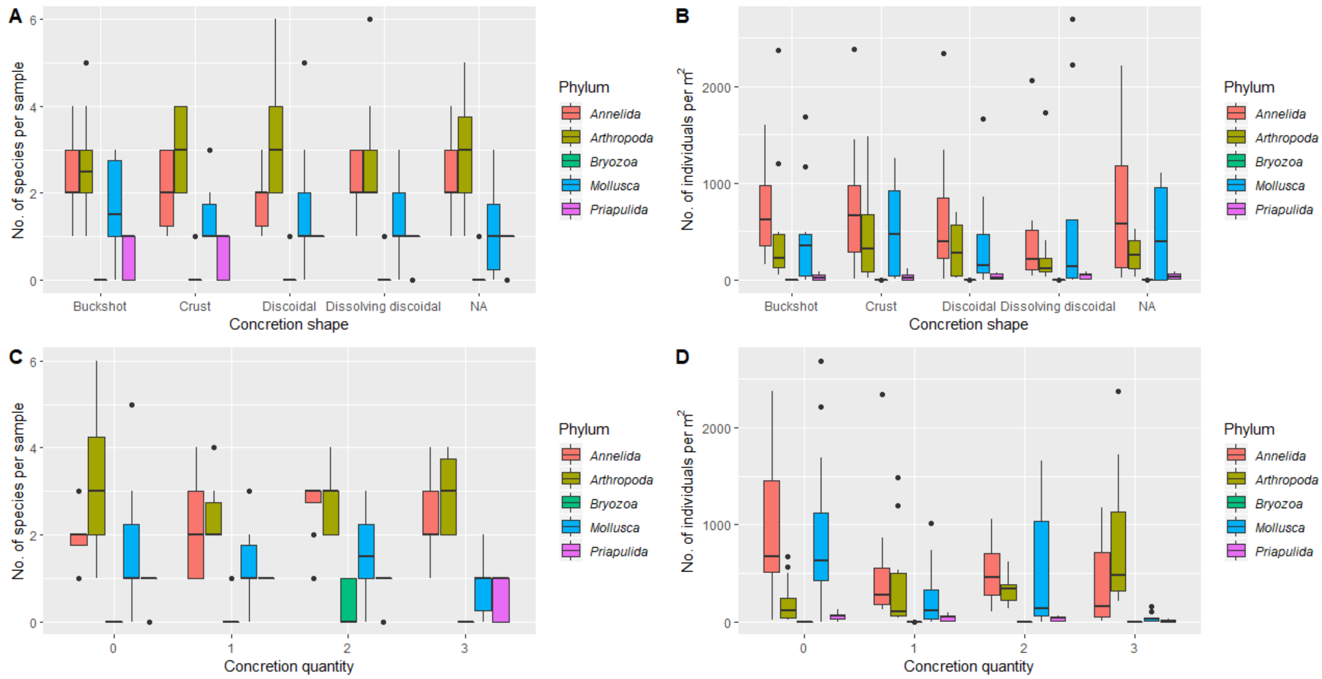

Figure 13. A) Number of species per sample vs. concretion shape. **B)** Number of individuals per m^2 vs. concretion shape. **C)** Number of species per sample vs. concretion quantity. **D)** Number of individuals per m^2 vs. concretion shape.

The community composition varied according to concretion shape and quantity (Table 7; Fig. 13). Both the mean number of species and the mean density of annelids were affected by concretion quantity; the densities were the highest on sites with low (1) concretion quantity (reference cites: 969.794 ind. m^{-2}, sites with low concretion quantity: 847.326 ind. m^{-2}). Yet, the mean number of species (2.625) was highest on sites with intermediate (2) concretion quantity. The highest densities of annelids were on sites with buckshot concretions (995.545 ind. m^{-2}). The mean number of arthropod species was higher on sites with discoidal (2.875) or crust (3.125) shaped concretions as well as reference sites. However, the mean arthropod density was greater on sites with high (3) concretion quantity (1328.571 ind. m^{-2}), as well as sites with crust shaped concretions (1582.589 ind. m^{-2}). Bryozoans were only observed on sites with discoidal concretions. Both the shape and the quantity of concretions affected mollusc densities; the highest mean densities were observed on sites with discoidal concretions (655.134 ind. m^{-2}) as well as reference sites (856.457 ind. m^{-2}). Priapulids were observed on all sites, but densities were higher in sites with discoidal (46.875 ind. m^{-2}) and dissolving discoidal (37.946 ind. m^{-2}) concretions, which were shallower sites of the study. Priapulid densities were also high on reference sites (49.110 ind. m^{-2}).

Discussion

The purpose of this study was to investigate the role of iron-manganese concretion fields as a component of Baltic Sea biodiversity. Iron-manganese concretions increase the complexity and geodiversity of the seafloor, and the aim was to study the effects of the increased seabed complexity on the macrobenthic community composition in the Gulf of Finland.

General Trends

Concretion fields increase seabed habitat complexity and therefore also influence the faunal composition of the deeper seabed areas of the Northern Baltic Sea. In previous research on habitat complexity, the general trend is that habitat complexity has a positive effect on biodiversity and abundance of fauna, regardless of the habitat type or the community composition (Kovalenko et al., 2012). As a habitat forming substrate for macrofauna, FeMn concretions are comparable to other hard substrates (e.g. discoidal concretions vs. gravel). Yet, cavernous crusts provide the invertebrates with additional topographical complexity with crevices and niches, offering microhabitats for fauna that is not typical for soft seafloor. Crusts also add to the surface area of the seafloor, supporting both a) microhabitat availability (MacArthur and MacArthur, 1961; Willis et al., 2005; Koivisto and Westerbom, 2010; Kovalenko et al., 2012), and b) increased surface area (Heck and Wetstone, 1977; Willis et al., 2005) hypothesis' in previous research on habitat complexity.

Regarding sessile and mobile fauna, the differences between concretion and reference sites are likely the result of higher hard substratum coverage on concretions sites. Hard substratum availability, including concretions, appears to have a more significant effect on the abundance of fauna as well as the total faunal coverage. The depth range of sessile and mobile fauna assessed in this study was approximately 10 – 23 m, and the concretions found in these depths were generally discoidal or irregular in shape, lying flat on the sediment surface. As a result, concretions do not seem to generate topographical heterogeneity. Furthermore, discoidal concretions do not seem to provide habitats for the seabed invertebrates that differ significantly from gravel or small stones, since the species observed growing on concretions (*E. crustulenta*, *C. caspia*) were also observed on other hard substratum types.

Both the shape and quantity of concretions had a positive effect on the number of species in sediment infauna. Sites with crusts or discoidal concretions seemed to affect the faunal composition of the seafloor more than spheroidal concretions. Crusts alter the topographical heterogeneity of the seafloor more than the concretion of other shapes; crusts form on top of each other, lifting a few centimetres from the bottom sediment. The topographical difference offered by discoidal or spheroidal concretions is typically no more than a few millimetres. Yet, compared to spheroidal or buckshot shaped concretions, discoidal concretions offer relatively stable substratum for sessile fauna.

Community Composition

The macrobenthos of the northern Baltic Sea typically consists of rather generalist than opportunist species, hence the analysis of community composition were based on phyla rather than functional groups (Bonsdorff and Pearson, 1999). Buckshot shaped or spheroidal concretions occurred on both the sediment surface as well as a few centimetres into the sediment column. No epifauna was observed on sites with buckshot concretions, and the species composition appeared to be similar with the sites without concretions. Compared to other concretions that occur on the sediment surface, buckshot shaped concretions do not offer the same stability as discoidal concretions or crusts as a substratum for faunal settlement (Walters and Wethey, 1996; Shunatova et al., 2018).

Sites with crust shaped concretions occurred generally deeper than sites with discoidal concretions. In addition to offering hard substratum on a predominantly soft seafloor, crusts pile up on top of each other, forming crevices that can offer shelter for fauna that is not typical for bare, soft seafloors. Sites with crust shaped concretions typically had more amphipods, such as *Pontoporeia femorata* and *M. affinis*. Of all the observations, *M. affinis* densities were the highest on these sites. For amphipods, crusts may offer shelter from predation, which supports the microhabitat availability hypothesis (Willis et al., 2005; Koivisto and Westerbom, 2010; Kovalenko et al., 2012). Crusts can also act as substratum for faunal settlement, as hard-substratum species *Mytilus trossulus x edulis* was found on these sites.

Bryozoan *E. crustulenta* was only observed on discoidal concretions. However, the depth range of the observations should be considered, as discoidal concretions (both whole and dissolving) were only observed in depths 23 m and above. The exact reason for the presence of the species only on one type of concretions is unclear – the distribution of a species is affected by various factors, such as temperature, oxygen and salinity which are associated with depth (Nikulina and Schäfer, 2006). *E. crustulenta* generally settles on shadowed rather than illuminated surfaces as a result of algal growth (Silén et al., 1972; Sokołowski et al., 2017), which should not, however, affect the settlement of the species in the depths of this study.

Different sedimentation and erosion rates and currents on different concretion sites may also affect species occurrence. Bivalve *L. balthica* commonly occurs on soft sediment seafloors, and its densities were the highest on reference sites. On concretion sites, the average densities were higher on sites with discoidal concretions. For burrowing bivalves, discoidal concretions offer the most suitable environment out of concretion fields: discoidal concretions lay flat on the sediment surface and offer batches of soft substratum on the sediment surface. Spheroidal concretions are gravel-like, coarse substratum which also affects the soft-sediment availability in the sediment, which may hinder the movement of bivalves. Crusts separate the sediment from the water column and may affect the food availability for burrowing bivalves (Tallqvist, 2001). The observed occurrence patterns of benthic organisms in this study are likely also affected by depth and oxygen availability (Villnäs et al., 2019). Generally, depth had a negative effect on both the number of observed species as well as the density of sediment infauna and the coverage of sessile fauna. FeMn concretions also host a specific microbiota, which alter the biogeochemical conditions of the seafloor (Yli-Hemminki et al., 2014), thus may affect the faunal composition associated with concretions (Veillette et al., 2007).

In general, sites with dissolving concretions had a lower abundance of fauna, possibly due to anoxia and the potential release of harmful substances (PAHs, crude oil) from the dissolving concretions (Reunamo et al., 2017). The faunal composition of these sites consisted of species resistant to low oxygen levels, such as polychaete worms of genus *Marenzelleria*, which are generally opportunist species and tolerate low oxygen concentrations (Schiedek, 1997; Kauppi et al., 2015). Dissolving concretions were found 6 – 8 cm deep in the sediment, so they should not have a significant effect on the faunal composition on top of the sediment.

Environmental Implications

The shape and quantity of concretions affects the composition of sediment infauna. Based on this study, the concretion fields should not necessarily be classified as one habitat type. Different concretion possess unique characteristics in both structural and chemical composition (Zhamoida et al., 2004), resulting in differences in the composition of associated macroinvertebrate communities. Sites with crust shaped concretions offer hard substratum for the settlement of *E. crustulenta* and *M. trossulus x edulis*, as well as shelter from predation in the crevices of coalescing concretions for arthropods, such as *P. femorata*, *M. affinis*. Seafloors with concretions of other shapes have greater soft sediment availability for infauna, yet the settlement of hard-substratum fauna is also possible on discoidal concretions.

Concretion fields are threatened by anoxia as well as anthropogenic activities on concretion fields. The role of different types of concretion fields should be considered when deciding on possible conservation, management or mineral extraction activities on concretion fields in the future. The microbiota associated with FeMn concretions plays a significant role in the degradation of PAHs and crude oil in the sediment (Reunamo et al., 2017), and concretions themselves bind large quantities of P and As (Zhamoida et al., 2007; Yli-Hemminki et al., 2016). FeMn concretions also form over long periods of time (Grigoriev et al., 2013) and as a result the recovery from possible mineral extraction operations may prove to be a really slow process (Zhamoida et al., 2017; Stratmann et al., 2018; Simon-Lledó et al., 2019). With the removal of concretions, the risk of biodiversity loss is significant, and the effects on the ecosystem may possibly irreversible in the Northern Baltic Sea. In case of possible economic utilization of FeMn concretions in the Gulf of Finland, the environmental and ecological effects of seabed mining should be thoroughly investigated (Kaikkonen et al., 2018).

Critical Assessment of the Study

The shape and abundance of concretions is a sum of various factors, such as currents, sedimentation and slope of the seafloor (Zhamoida et al., 1996, 2004). Concretions form over a long period of time, during centuries, and the presence of concretions or the shape of the concretions present usually is a result of differences among the environmental conditions among different sites. Macrobenthic communities of the Baltic Sea are also affected by the variability of environmental conditions, and some of the differences may be a result of this variability (Kaller and Hartman, 2004; Jones et al., 2012; Herkül et al., 2016). In addition to habitat heterogeneity, species distribution is affected by salinity, oxygen availability, and primary productivity (Bonsdorff and Pearson, 1999; Laine, 2003). The combined effects of these factors are yet to be investigated.

Sessile and mobile fauna assessment was conducted in two parts: one in June and one in August. The data gathered from VELMU also included observations conducted in July. A succession of *C. caspia* was observed from the data, as no hydroid colonies were observed in June. In July, some polyp observations were made (VELMU data included) and by August most sites had polyps growing on hard surfaces. Observations coincide with previous observations on *C. caspia* life cycle (Jormalainen et al., 1994). No other clear succession was observed based on the data of this research; however, it does not implicate that no other species' seasonal succession did not happen on the studied sites. The study could have been conducted in one part, and, in this case, the reference data from VELMU could have been gathered from a smaller time frame.

Much of the previous research on habitat complexity investigates the effects of this phenomenon on fish communities. However, the assessment of the effects of FeMn concretions on fish proved unsuccessful in this study. The only species present were bottom-dwelling fish: viviparous eelpout (*Zoacres viviparus*), and gobies of genus *Pomatoschistus*. Concerning mobile fauna assessment, SCUBA diving is an invasive method that may affect the behaviour of fish (Barker et al., 2011; Titus et al., 2015), and it may not be the best method for observing fauna that can escape the approaching divers in poor visibility. However, diving on-site usually offers the most cost-effective assessments with accurate identifications of species (Grane-Feliu et al., 2019). The inference of bubbles from open circuit breathing apparatus' might be solved by using closed circuit breathing apparatus' instead (Gray et al., 2016).

For this study, reference data was gathered from HERTTA database and the previous observations from VELMU inventory programme. Finding suitable reference data proved moderately challenging; observations with suitable bottom substrate (small grain size, e.g. clay) were only made in depths 23 – 30 m. In addition, observer bias could not be measured. There were also some differences in sampling methods: on MERISAMPO project, duplicates from each sediment sample were collected, while in HERTTA samples consisted of only one sample taken from each site. With the data gathered from VELMU, there were no substrate specific observation of benthic fauna or fish. Observations in the MERISAMPO project were conducted with point dives instead of line-transects. The observations conducted in the VELMU are mostly conducted with line-transects, but for irregularly shaped concretion fields they deemed ineffective and time-consuming. The reference data could have also been collected during the project, to eliminate these issues.

Conclusions

The shape and quantity of iron-manganese concretions affect the macroinvertebrate communities on the seafloor. Similarities to the invertebrate composition of soft sediment habitats depends on the soft sediment availability in the habitat, which is affected by concretion shape and quantity. Concretions offer both hard substratum for faunal settlement, as well as microhabitats in form of crevices. As the size of the concretions increases, their contribution to the complexity of the seafloor increases as well. Crusts seem to offer the most complex habitats differing significantly from the other concretion habitats. Based on this study, concretion fields should not necessarily be considered as just one habitat type, since the faunal composition appears to differ according to the shape of the concretions.

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Appendix 1. Sessile and mobile fauna data

							Substratum coverage (%)												Species coverage (%)																	
ID	Commune	Type	Organization	Project	Date	Depth (m)	Rock	Boulder > 3000 mm	Boulder 1200-3000 mm	Boulder 600-1200 mm	Large stone 100-600 mm	Small stone 60-100 mm	Gravel 2,0-60 mm	Sand 0,06-2,0 mm	Silt 0,002-0,06	Clay < 0,002 mm	Mud <0,002 mm	Concretions	*Amphibalanus improvisus*	*Cerastoderma glaucum*	*Bivalve shells*	*Cordylophora caspia*	*Dreissena polymorpha*	*Einhornia crustulenta*	*Embletonia pallida*	*Limecola balthica*	*Mya arenaria*	*Mytilus trossulus x edulis*	*Mytilus spp. shells*	*Polyps*	*Saduria entomon*	*Worm pipes*	*Pisces spp.*	*Pomatochistus spp.*	*Zoarces viviparus*
ESLP_5466	HKI	Ref	MH	VELMU	2014-07-08	10.30					1		1	98					0.2		4.9									0.1					
ESLP_5556	PRV	Ref	MH	VELMU	2014-07-09	14.00					5	5	10	80					2		4			1				2		0.25					
ESLP_5646	PRV	Ref	MH	VELMU	2014-07-09	11.00							2	98							0.1							0.98	0.1						
ESLP_5650	PRV	Ref	MH	VELMU	2014-07-09	12.00						1	1	98							0.1							0.98	0.1	0.001					
ESLP_6630	PRV	Con	MH	VELMU	2014-07-21	12.40	30				20							50	6.5	0.1		12.5			3			17.5							1
ESLP_6634	PRV	Con	MH	VELMU	2014-07-21	14.00	20				20							60	20	0.1		5		5		0.1		15							
ESLP_6638	PRV	Con	MH	VELMU	2014-07-21	16.60	50											50	5			10		1				5							
ESLP_8241	KTA	Ref	KASEL	VELMU	2014-08-04	13.00					10	8	2	80					1		0.001	0.1	0.1	0.1											
ESLP_9841	RAA	Ref	MH	VELMU	2014-08-25	14.00					5	5	10		80						4	2											2		
ESLP_9844	RAA	Ref	MH	VELMU	2014-08-25	15.00							5		95							4.75													
K2.1	EPO	Ref	SYKE	MERISAMPO	2019-06-14	10.7					30		70						10	0.001				0.001		5		0.001							
K2.2	EPO	Con	SYKE	MERISAMPO	2019-06-14	10.3				20	35	10	30					5	5	0.001						5								4	
K2.3	EPO	Con	SYKE	MERISAMPO	2019-06-14	10.2					10	40	40					10	10					0.001		1									1
K4.1	EPO	Con	SYKE	MERISAMPO	2019-06-11	22.8										65		35		5											3				
K4.2	EPO	Con	SYKE	MERISAMPO	2019-06-11	22.5										60		40			5										4				
K4.3	EPO	Con	SYKE	MERISAMPO	2019-06-11	22.5										60		40			5										3				
K5.1	EPO	Con	SYKE	MERISAMPO	2019-06-11	17.2							70		10			20		5															
K5.2	EPO	Con	SYKE	MERISAMPO	2019-06-11	17.6							65		5			30			5														
K5.3	EPO	Con	SYKE	MERISAMPO	2019-06-11	17.5							70					30						0.001											
Ka1.1	HKI	Con	SYKE	MERISAMPO	2019-08-06	16								90				10								5					2	10		1	
Ka1.2	HKI	Con	SYKE	MERISAMPO	2019-08-06	15.8							5	25				70				2				5	1					15			
Ka1.3	HKI	Con	SYKE	MERISAMPO	2019-08-06	15.8								70				30				2				5		1			1	10		1	
Ka2.1	HKI	Con	SYKE	MERISAMPO	2019-08-06	15.4					10					85		5	1							1					1	5			
Ka2.2	HKI	Con	SYKE	MERISAMPO	2019-08-06	15.5				20						75		5	15	1		10				5						5			
Ka2.3	HKI	Con	SYKE	MERISAMPO	2019-08-06	15.5				10	20					60		10	10			15		1		5		5				5			
Ka3.1	HKI	Ref	SYKE	MERISAMPO	2019-08-06	12.2									100											1	1								
Ka3.2	HKI	Ref	SYKE	MERISAMPO	2019-08-06	11.8								100												1	0.001					5			
Ka3.3	HKI	Ref	SYKE	MERISAMPO	2019-08-06	12.1								100												1						20			
Ky1.1	EPO	Con	SYKE	MERISAMPO	2019-08-07	19.9							10	85				5				1		0.001		5		5				10		1	
Ky1.2	EPO	Con	SYKE	MERISAMPO	2019-08-07	20.5	30						20	40				10	5			5						10				10			2
Ky1.3	EPO	Con	SYKE	MERISAMPO	2019-08-07	20.1							20	79				1	1									10				5			
Ky2.1	EPO	Ref	SYKE	MERISAMPO	2019-08-07	22.4								100												0.001									
Ky2.2	EPO	Con	SYKE	MERISAMPO	2019-08-07	21.5								99				1								5					4				
Ky2.3	EPO	Ref	SYKE	MERISAMPO	2019-08-07	22.2								100												0.001					1				
VELMU2015_2434	HMA	Con	MH	VELMU	2015-08-04	11.30					15				25			60	1.5											3					
VELMU2015_2439	HMA	Con	MH	VELMU	2015-08-04	11.60					30		30		20			20	3					1.5	1.5					4.5					
VELMU2015_2448	HMA	Con	MH	VELMU	2015-08-04	11.90									25	25		50								2				10					
VELMU2015_2578	RAA	Ref	MH	VELMU	2015-06-10	10.20					1				99				0.1					0.1											
VELMU2015_2581	RAA	Ref	MH	VELMU	2015-06-10	10.40					2				98				0.1	0.001				0.1		0.001		0.1							
VELMU2015_3081	IKO	Ref	MH	VELMU	2015-07-15	17.80					5				50		45											0.1			1				
VELMU2015_3085	IKO	Ref	MH	VELMU	2015-07-15	19.60									50		50																		
VELMU2015_3088	IKO	Ref	MH	VELMU	2015-07-15	19.60									50		50									0.1									
VELMU2015_3092	IKO	Ref	MH	VELMU	2015-07-15	19.60					1				49		50		0.1					0.1				0.1							
VELMU2015_3095	IKO	Ref	MH	VELMU	2015-07-15	19.60									50		50											0.1			1			2	
VELMU2015_3098	IKO	Ref	MH	VELMU	2015-07-15	19.60									50		50																		
VELMU2015_3434	KKN	Ref	MH	VELMU	2015-08-06	12.80					5		2	93					0.1	0.1		1.25				0.1		4.9			1				
VELMU2015_4019	EPO	Ref	MH	VELMU	2015-08-04	15.90					2		8	90														0.68							

Species presence = 0.001 coverage (%). Organization abbreviations: KASELY = ELY-Centre of South-East Finland, MH = Metsähallitus, SYKE = Finnish Environment Institute. Commune abbreviations: HMA = Hamina, IKO = Inkoo, EPO = Espoo, HKI = Helsinki, KKN = Kirkkonummi, KTA = Kotka, PRV = Porvoo, RAA = Raasepori.

Appendix 2. Sediment infauna data

ID	Commune	Type	Sieve	Depth m	Concretion quantity	Concretion shape	Date	*Bylgides sarsi*	*Calliopius laeviusculus*	*Cerastoderma glaucum*	*Chironomidae*	*Copepoda*	*Corophium*	*Corophium volutator*	*Einhornia crustulenta*	*Gammarus spp.*	*Halicryptus sppinulosus*	*Hediste diversicolor*	*Hydrobia*	*Jaera spp.*	*Limapontia capitata*	*Limecola balthica*	*Marenzelleria spp.*	*Monoporeia affinis*	*Mysis mixta*	*Mysis relicta*	*Mytilus trossulus*	*Nematoda*	*Neomysis integer*	*Oligochaeta*	*Ostracoda*	*Polychaeta*	*Pontoporeia femorata*	*Potamopyrgus antipodarum*	*Saduria entomon*	*Theodoxus fluviatilis*
Herröfjärden (Wp226)	KKN	Ref	0.5	23	0	NA	2014-07-24			43.290							86.580					1601.732	2034.632	389.610						346.320				43.290		
Herröfjärden (Wp226)	KKN	Ref	1	23	0	NA	2014-07-24			43.290							86.580					1082.251	1341.991	216.450										43.290		
Itäinen ulkosaar_1142	HKI	Ref	0.5	28	0	NA	2014-09-02									6.001	120.012			3.000		2688.269	1743.174	180.018						471.047	129.013				18.002	
Itäinen ulkosaar_1142	HKI	Ref	1	28	0	NA	2014-09-02										69.007					822.082	567.057	147.015						63.006					18.002	
Katajaluoto_125	HKI	Ref	0.5	27	0	NA	2014-11-21				3.000			12.001			72.007		3.000		24.002	786.079	1107.111	21.002			3.000			957.096	639.064			45.005		
Katajaluoto_125	HKI	Ref	1	27	0	NA	2014-11-12										63.006		3.000			600.060	516.052	21.002						66.007	3.000			21.002		
Katajaluoto_1259	HKI	Ref	0.5	29	0	NA	2014-11-12							12.001		3.000	78.008	3.000				984.098	1419.142	24.002			6.001			177.018				3.000	12.001	
Katajaluoto_1259	HKI	Ref	1	29	0	NA	2014-11-12							6.001			60.006	3.000				486.049	633.063	24.002			3.000			3.000					12.001	
Katajaluoto_1259	HKI	Ref	0.5	29	0	NA	2015-09-29										27.003					1254.125	282.028	15.002	3.000				6.001	51.005	468.047			6.001	3.000	
Katajaluoto_1259	HKI	Ref	1	29	0	NA	2015-09-29															477.048	123.012	15.002	3.000					3.000					3.000	
Knaperskär_147	EPO	Ref	0.5	24	0	NA	2014-09-16				9.001						66.007					630.063	1293.129	72.007		3.000	3.000		3.000	201.020	9.001				27.003	
Knaperskär_147	EPO	Ref	1	24	0	NA	2014-09-16				6.001						27.003					318.032	609.061	66.007		3.000	3.000			90.009	6.001				27.003	
Knaperskär_147	EPO	Ref	0.5	25	0	NA	2015-09-22										66.007			3.000		630.063	879.088	81.008						48.005	30.003				9.001	
Knaperskär_147	EPO	Ref	1	25	0	NA	2015-09-22										9.001					435.044	294.029	81.008											9.001	
MS1.1	HKI	Con	0.5	52	3	BU	2019-06-17	8.929	17.857								8.929						732.143	392.857								0.009				
MS1.1	HKI	Con	1	52	3	BU	2019-06-17															8.929	1178.571	187.500							26.786	0.009				
MS1.2	HKI	Con	0.5	52	2	BU	2019-06-17	8.929				35.714											1000.000	357.143								0.009				
MS1.2	HKI	Con	1	52	2	BU	2019-06-17										8.929					17.857	1053.571	232.143								0.009			17.857	
MS2.1	HKI	Con	0.5	48	3	CR	2019-06-18		62.500								8.929					26.786	205.357	687.500							1625.000	0.009				
MS2.1	HKI	Con	1	48	3	CR	2019-06-18		107.143								8.929					35.714	8.929	339.286									8.929		26.786	
MS2.2	HKI	Con	0.5	48	3	CR	2019-06-18																98.214	178.571							142.857	0.009				
MS2.2	HKI	Con	1	48	3	CR	2019-06-18															26.786	8.929	214.286								0.009			26.786	
MS3.1	HKI	Con	0.5	42	3	CR	2019-06-17	17.857	98.214								26.786					26.786	785.714	2500.000						17.857	3080.357	0.009	8.929			
MS3.1	HKI	Con	1	42	3	CR	2019-06-17		125.000								17.857					133.929	35.714	875.000			17.857			8.929		0.009	53.571		80.357	
MS3.2	HKI	Con	0.5	42	3	CR	2019-06-17	8.929				8.929					17.857						607.143	660.714							1053.571	0.009				
MS3.2	HKI	Con	1	42	3	CR	2019-06-17	17.857	35.714													89.286	53.571	589.286			8.929								71.429	
MS5.1	EPO	Con	0.5	23	1	DS	2019-06-18							8.929			62.500					62.500	178.571	232.143						17.857	285.714	0.009				
MS5.1	EPO	Con	1	23	1	DS	2019-06-18	8.929							0.009		62.500					1000.000	116.071	71.429						35.714		0.009		8.929	35.714	
MS5.2	EPO	Con	0.5	23	2	DS	2019-06-18										62.500					89.286	205.357	160.714						98.214	196.429	0.009	26.786			
MS5.2	EPO	Con	1	23	2	DS	2019-06-18								0.009		44.643					1089.286	80.357	80.357			71.429			8.929		17.857		8.929	53.571	
MS6.1	EPO	Con	0.5	23	2	DS	2019-06-18										53.571			8.929		71.429	392.857	223.214						214.286	133.929	0.009				
MS6.1	EPO	Con	1	23	2	DS	2019-06-18								0.009		8.929			17.857		910.714	196.429	98.214			53.571								26.786	26.786
MS6.2	EPO	Con	0.5	23	2	DS	2019-06-18										53.571			17.857		169.643	303.571	98.214			17.857			133.929	500.000	0.009				
MS6.2	EPO	Con	1	23	2	DS	2019-06-18		62.500						0.009		26.786			17.857		1553.571	464.286	187.500			107.143			17.857		0.009			44.643	
MS7.1	EPO	Con	0.5	29	1	D.DS	2019-06-19										8.929						276.786	71.429							17.857	0.009				
MS7.1	EPO	Con	1	29	1	D.DS	2019-06-19										8.929					142.857	125.000	35.714											8.929	
MS7.2	EPO	Con	0.5	29	1	D.DS	2019-06-19										89.286						866.071	303.571							107.143					
MS7.2	EPO	Con	1	29	1	D.DS	2019-06-19										8.929					151.786	178.571	35.714									35.714		17.857	
MS8.1	EPO	Con	0.5	25	1	D.DS	2019-06-19										53.571					8.929	2116.071	80.357						223.214	1116.071	0.009				
MS8.1	EPO	Con	1	25	1	D.DS	2019-06-19				8.929						8.929			8.929		348.214	553.571	8.929										17.857	8.929	26.786
MS8.2	EPO	Con	0.5	25	1	D.DS	2019-06-19										89.286					62.500	3125.000	205.357			8.929			196.429	1276.786	0.009		17.857		
MS8.2	EPO	Con	1	25	1	D.DS	2019-06-19										35.714					732.143	446.429	8.929						8.929					44.643	
P102	KKN	Ref	0.5	26	0	NA	2014-08-01				18.657		9.328	27.985			27.985					2220.149	1156.716	9.328		9.328		9.328		167.910	485.075					
P102	KKN	Ref	1	26	0	NA	2014-08-01							27.985			27.985					1100.746	447.761			9.328				121.269						
Salmen NE 207	KKN	Ref	0.5	30	0	NA	2013-05-20																111.940	9.328							9.328				9.328	
Salmen NE 207	KKN	Ref	1	30	0	NA	2013-05-20																18.657	9.328											9.328	
StorMickelskär_123	KKN	Ref	0.5	27	0	NA	2015-09-29										72.007					402.040	1386.139	90.009						60.006	27.003				15.002	
StorMickelskär_123	KKN	Ref	1	27	0	NA	2015-09-29										24.002					315.032	591.059	90.009											15.002	

The data in this appendix is given as individuals m^{-2}. Commune abbreviations: EPO = Espoo, HKI = Helsinki, KKN = Kirkkonummi.